Reconstructing cave bear paleoecology from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz Cave, Turkey

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Abstract.—Cave bears, an extinct subgenus (*Spelearctos*) of *Ursus*, were versatile enough to inhabit large areas of the northern hemisphere during the middle and late Pleistocene, yet they had evolved a specialized dentition that emphasized grinding functions, implying a heavy dietary reliance on tough, fibrous foods (i.e., plants). Isotope studies have yielded conflicting results on cave bear diet, however, often without consideration of the provenance of the samples or the possible contradictions that taphonomic and morphologic evidence might pose to dietary interpretations. It is likely that cave bear habits varied somewhat in response to environmental circumstance, and the limits on their abilities to do so remain unknown. If the larger goal of paleontological inquiry is to reconstruct the adaptations of cave bear species, then variation and commonalities among populations must be tracked closely, and the disparate lines of evidence currently available examined together on a case by case basis. Clearly, no single analytical technique can achieve this. By way of example we present the results of a cross-disciplinary collaboration that combines osteometric, isotopic, and taphonomic approaches to studying the paleoecology of a bear assemblage from Yarimburgaz Cave in northwest Turkey. Reference information on the linkages between diet, hibernation, and population structure in modern bears provides test implications for the investigation. Osteometric techniques demonstrate the presence of two coextant middle Pleistocene bear species in the sample—*Ursus (Spelearctos) deningeri*, a form of cave bear, and *U. arctos* or brown bear—the former abundant in the sample, the latter rare. An attritional mortality pattern for the bears and the condition of their bones show that most or all of the animals died in the cave from nonviolent causes in the context of hibernation. The study also elucidates several characteristics of the cave bear population in this region. Osteometric techniques show that the adult sex ratio of the cave bears is only slightly skewed toward females. This pattern lies near one extreme of the full range of possible outcomes in modern bear species and can only reflect a strong dietary dependence on seasonally available plants and invertebrates, showing that hibernation was a crucial overwintering strategy for both sexes; the results specifically contradict the possibility of regular, heavy emphasis on large game (hunted or scavenged) as a winter food source. The nature of wear and breakage to the adult cave bear teeth indicates that food frequently was obtained from cryptic sources, requiring digging and prying, and that extensive mastication was necessary, leading to complete obliteration of some cheek tooth crowns in old individuals. The patterns of tooth damage during life corroborate the dietary implications of the adult sex ratio and also argue for a diet rich in tough, abrasive materials such as nuts, tubers, and associated grit. The carbon and oxygen isotopic compositions of cave and brown bear tooth enamel from the site are virtually identical, and there is no evidence of a strong marine signal in either species, despite the cave's proximity to a modern estuary of the Sea of Marmara; nitrogen isotope ratios could not be examined because of poor protein preservation. The isotope results suggest that both bear species were highly omnivorous in the region during the middle Pleistocene and obtained nearly all of their food from terrestrial and fresh-water habitats. Bone pathologies, usually originating from trauma, occur in some of the adult bears, testifying to long lifespans of some individuals in this fossil population. The Yarimburgaz cave bears also exhibit great size dimorphism between the sexes, based on weight-bearing carpal bone dimensions, with adult males attaining roughly twice the body mass of adult females.

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Introduction

Cave bears are an extinct form of bear that achieved wide distribution in Eurasia during the middle and late Pleistocene, especially in regions lying between the 55° and 35° parallels of the northern hemisphere (as summarized by Kurtén 1976; Baryshnikov 1997). The best known species of cave bear are *Ursus (Spelearctos) deningeri* and *Ursus (Spelearctos) spelaeus*. They are considered chronospecies (ancestor

and descendent) whose existences spanned the Middle and Late Pleistocene respectively (e.g., Kurtén 1976: pp. 41–45). A third species of separate ancestry, *Ursus (Spelearctos) rossicus*, is also known (Baryshnikov 1997). The presence of cave bear remains in Pleistocene deposits of southern Britain, most of mainland Europe (Kurtén 1976), the Caucasus, western and central Asia, the Urals, and in the case of *U. rossicus* also southwestern Siberia (Baryshnikov 1989, 1996, 1997), demonstrates that these animals were able to adjust to a great variety of Pleistocene environments.

Nonetheless, extensive research on the dentitions and skull architecture of cave bears reveals unique masticatory specializations, apparently for processing tough, abrasive foods (e.g., Koby 1940; Kurtén 1976; Baryshnikov 1996, 1997). The extent to which cave bears were carnivorous, and whether they obtained meat and dietary fats from seasonally available invertebrates and small vertebrates or from large mammals, remain open questions. Recent isotope studies of skeletal samples from modern and Pleistocene bear species have begun to enrich investigations of cave bear diet (e.g., Matheus 1995; Hilderbrand et al. 1996), but the results often are confusing, partly because isolated cases are assumed to represent a uniform condition for entire species (e.g., Hilderbrand et al. 1996), and partly because isotope results seldom are integrated with other, independent sources of data.

The sum total of available information on cave bears already suggests that their diets varied from one Pleistocene population to the next (compare Kurtén 1976; Bocherens et al. 1994; Hilderbrand et al. 1996; Baryshnikov 1997; and our results below). This variation among local situations is difficult to interpret, because its net importance has yet to be scaled to the well-documented trajectory in the dental evolution of cave bears. At least two issues of research design are integral for expanding the knowledge envelope on cave bear paleoecology: (1) Similar batteries of tests eventually need to be applied to cases throughout the entire Pleistocene range of the cave bears, with the geographic provenance of any one sample being an important qualifier of the results obtained. (2) Disparate lines of evidence concerning the lifeways of cave bears, such as from taphonomic, osteometric, and isotope analyses, require conceptual integration in order to be most effective for addressing questions about the ecology of the extinct bear species. It is clear that no single family of analytical techniques currently possesses this ability. New information can be gained when they are used together, however, mainly because the nature of contradictions and agreements can be explored.

We do not propose to take on both issues at once—the first is a particularly humbling enterprise. Rather, we focus on the second issue, using for our example a large death assemblage of bears from middle Pleistocene deposits in Yarimburgaz Cave in northwest Turkey. This cross-disciplinary collaboration integrates findings from osteometric, isotopic, and selected taphonomic analyses. Of wider interest are the means by which independent sources of information from skeletons are integrated to reveal aspects of the resource ecology of two species: *Ursus (= Spelearctos) deningeri*, a common and large form of cave bear, and the much less common *U. arctos* or brown bear. These bears once coexisted in northwestern Turkey and elsewhere in Eurasia, regions where only the brown bear survives today. Our analyses center on the more abundant cave bear remains. Because foraging habits, hibernation habits, and reproductive characteristics are strongly interlinked in modern bear species (reviewed by Kurtén 1976; Stiner et al. 1996; Stiner 1998), rules governing these basic connections can be used to investigate the adaptations of extinct bears.

The case we have chosen to investigate, from Yarimburgaz Cave in northwest Turkey, is also of interest for its unique qualities; Pleistocene cave bear populations from this region are poorly known, yet cave bears probably were once prevalent. The locality lies south of most or all previously documented cave bear sites save one in northern Israel (Tchernov and Tsoukala 1997).

The methods of analysis vary among sections of this article, and we therefore describe them with the corresponding results. We use osteometric measurements of teeth to evaluate the taxonomic status of the Yarimburgaz bears, independently of geochronologic and absolute
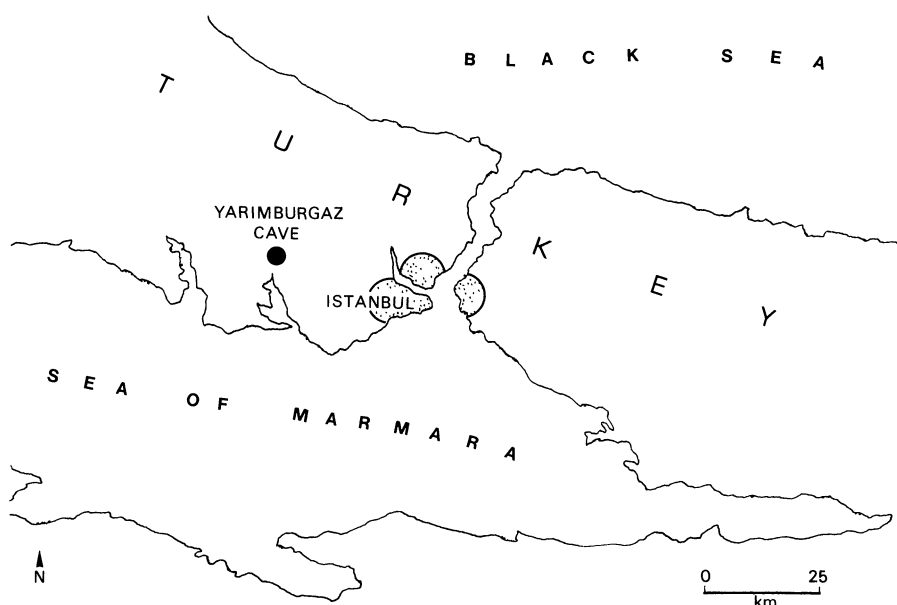
FIGURE 1.   Location of Yarimburgaz Cave in northwest Turkey, roughly 25 km west of the Bosporus Strait.

dating results—an important issue for cave bear taxonomy and biogeography. We use canine and second lower molar measurements to isolate the adult sex ratio of the cave bears, which for reasons explained below relates to the seasonal nature of cave bear diet in the study area. We then compare the carbon and oxygen isotopic compositions of 23 cave and brown bear tooth enamel samples in search of evidence for niche differentiation between the two species. The question of terrestrial versus marine dietary emphasis is also addressed in light of the cave's modern proximity to an estuary on the Sea of Marmara. We describe cave bear tooth damage and bone pathologies and explore their implications for foraging habits and individual longevity. Selected information published elsewhere on the Yarimburgaz cave bears is summarized as relevant to the discussion below, including the macromammal species found together in the deposit, and, for the cave bears, the mortality profile (from Stiner 1998), skeletal completeness, and the causes of bone damage (from Stiner et al. 1996).

Background to the Yarimburgaz Sample

Yarimburgaz Cave lies at the junction of western Asia and central Europe (Fig. 1), just west–southwest of both the Bosporus Strait and the modern Turkish city of Istanbul, and near the head of a small estuary that empties into the Sea of Marmara. The cave consists of two large chambers, the lower of which extends some 600 meters into a limestone hillside flanking the Sazlidere River valley. Middle Pleistocene faunal assemblages were recovered by F. C. Howell and G. Arsebük from extensive excavations of the lower chamber (Özdogân and Koyunlu 1986; Arsebük et al. 1990, 1991; Howell and Arsebük 1989, 1990; Arsebük and Özbaşaran 1994; Stiner et al. 1996). The fauna is especially rich in cave bear remains (93% of all identified specimens), accompanied by scant remains of various other large mammals (Table 1).

Most of the skeletal remains in the Yarimburgaz sample are easily identified to genus if not species, owing to a comparatively low degree of fragmentation and the excellent preservation of macroscopic features. The non-ursid mammals found in the Middle Pleistocene deposit include horse (*Equus caballus*), possibly wild ass (*E. hemionus?*), roe deer (*Capreolus capreolus*), fallow deer (*Dama* sp.), red deer (*Cervus elaphus*), giant deer (*Megaloceros* sp.), aurochs (*Bos primigenius?*), bison (*Bison* sp.), wild pig (*Sus scrofa*), wild goat and/or ibex (*Capra aegagrus, C. ibex*), and possibly gazelle

TABLE 1. Summary of macromammal specimen and stone artifact counts from the middle Pleistocene deposits of Yarimburgaz Cave excavated during 1988–1990.

Macromammal group	Tooth speci-mens	Bone specimens	Total specimens	% Total speci-mens
a. Macromammal tooth and bone counts				
Herbivores	42	109	151	4
Bears	761	3159	3920	93
Non-ursid carnivores	33	79	109	3
Total	836	3344	4180	100
b. Lithic artifact counts				
Retouched pieces			602	
Total lithic artifacts			1674	

Note: See Stiner et al. (1996: Appendixes 1 and 2) for a complete account of taxonomic and body-part representation of the mammalian species.
Source: Kuhn et al. 1996.

(*Gazella* sp.) and an undetermined species of megafauna (rhinoceros?). Carnivores other than bears constitute only 3% of the faunal assemblages (Table 1) and include large and small cats of the genera *Panthera* (*P. leo*, possibly also *P. pardus*) and *Felis* (*F. caracal* and *F. sylvestris*), hyena (*Crocuta?*), wolf (*Canis lupus*), fox (*Vulpes vulpes*), possibly dhole (*Cuon/Xenocyon*) and jackal (*Canis aureus?*), and a small species of *Mustela*. A full accounting of species abundances and bone element representation is provided in Stiner et al. (1996: Appendixes 1 and 2). The excavations also yielded substantial quantities of Paleolithic stone artifacts in the same layers (Kuhn et al. 1996).

In marked contrast to the condition of the other species' remains, bears occur as nearly complete but mostly disarticulated skeletons (Stiner et al. 1996). As many as 42 individual bears are represented in the middle Pleistocene sample excavated during 1988–1990 alone. It is clear from the taphonomic investigations (Stiner et al. 1996) that Yarimburgaz Cave was occupied alternately by hominids and large carnivores, especially cave bears. The close stratigraphic and horizontal associations of bear remains, Paleolithic tools, and non-ursid carnivore remains in the cave sediments are the result of largely unrelated depositional events. Co-occurrence of these materials is explained by space constraints imposed by the chamber walls, slow sedimentation rates relative to biogenic deposition, and localized jumbling of material by bears as they prepared winter bedding areas. The com-

plete, or nearly complete, bear skeletons accumulated in the cave as the result of hibernation-related mortality over many generations (see also Gargett 1996 on the case of Pod Hradam). The herbivore (ungulate) remains were brought to the cave primarily by non-ursid carnivores and, less frequently, pre-modern humans—not by bears.

Two Bear Species

Size comparisons of cheek teeth and fused (adult) bone elements testify to the presence of two distinct bear species in the middle Pleistocene deposits of Yarimburgaz Cave. Inter-individual variation in premolar and molar sizes in a population should be continuous between the sexes. Measured specimens lying well outside of that size distribution therefore can only represent a different species. The only teeth that pose an important exception to this rule are the permanent adult canines, whose dimensions can be quite different in the adult females and males of a given population (see below). Measurement orientations for teeth are illustrated in Figure 2 and follow conventions established by Driesch (1976: Fig. 16).

The size distribution for the lower second molars of the bears, shown in Figure 3, is based on anterior-posterior length (L) and bucco-lingual breadth (B). The data represent only those specimens for which reliable measurements could be taken in two dimensions. Brown bear teeth fall below the maximum (mean) proportional size difference that can be expected between the sexes in terrestrial mammals (roughly males/females = 1.45–1.50 by a linear standard [Dong 1997]). It is clear from the distribution that two bear species are represented in the assemblage, the smaller of which is quite rare (1–2% of all individuals) and whose tooth size lies more than three standard deviations from the mean in both dimensions. The results for M_2 typify those for the M_1, M_3, and M^1 as well. The size contrast between the two species is also apparent from various foot bones of adult bears, such as the fifth metacarpals shown in Figure 4.

The small bear is almost certainly *U. arctos*. The larger species, which constitutes the great majority of bear remains, is a form of cave bear. There is some question, however, as to
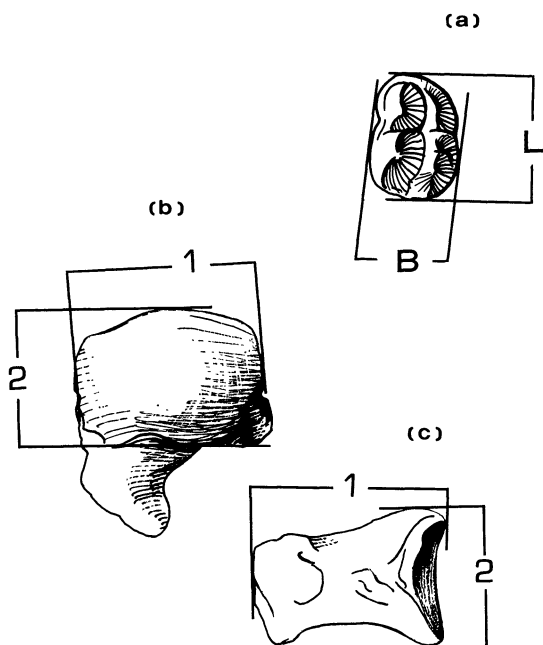
(a)

(b)

(c)

FIGURE 2. Placements and orientations of tooth and carpal measurements. A, Anterior–posterior (L) and buccolingual (B) dimensions of permanent premolars and molars, with calipers touching both cusps on the buccal face (following Driesch 1976). B, Measurements 1 and 2 on the scapholunate as shown in dorsal view. C, Measurements 1 and 2 on the pisiform, in ventral view.

whether it is *U. deningeri* or *U. spelaeus*. The cave bear cheek tooth samples from Yarimburgaz range from 25 to 64 measurable specimens, depending on element, and therefore permit statistical comparisons to other Pleistocene cave bear assemblages. (The measurement data are available on request from the first author.)

Tables 2 and 3 list summary statistics for length (L) measurements of the cheek teeth, excluding the specimens attributed to *U. arctos*. Mean lengths of the Yarimburgaz cave bear teeth are compared in Figure 5A and 5B to a variety of paleontological populations from Greece, France, and Germany compiled by Prat (1988: p. 295; but also see Schütt 1968; Laville et al. 1972; Kurtén 1973; Prat 1976; Prat and Thibault 1976; Argant 1980; Kurtén and Poulainos 1981) and from the Kudaro 1 and 3 Caves in the Transcausasus as compiled by Baryshnikov (1997). By way of background, the youngest (Late Pleistocene) form of the cave bear, *U. spelaeus*, was the largest, although its dimensions only slightly exceeded those of the Middle Pleistocene *U. deningeri*. Both were much larger, however, than *U. etruscus*, the Early Pleistocene ancestor. The mean
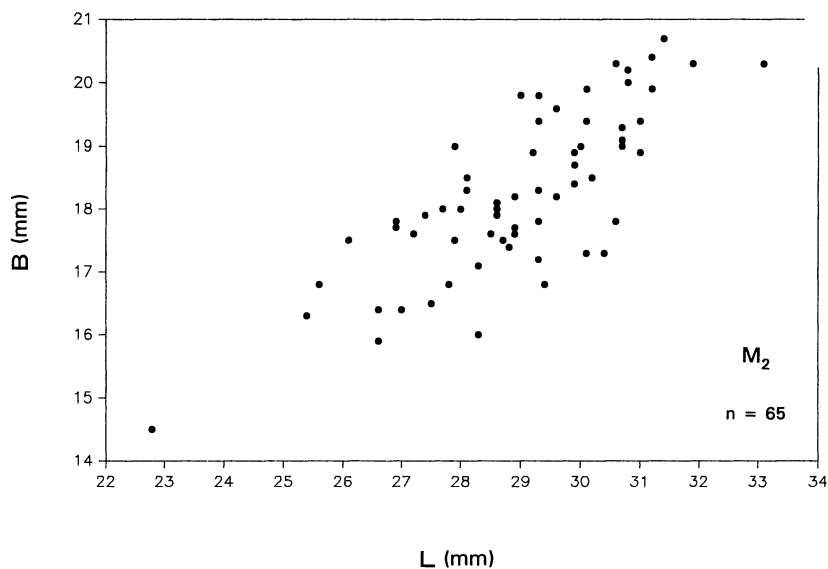

L (mm)

FIGURE 3. Scatter plot of length (L) and breadth (B) measurements for right and left bear mandibular second molars (M_2) from the Middle Pleistocene bear sample from Yarimburgaz Cave. The distribution reveals the presence of two species of *Ursus*, most remains of which represent *U. (Spelearctos) deningeri*, but one individual of *U. arctos* is also indicated by the point stranded near the graph intercept, which lies more than three standard deviations from the mean in both dimensions. Each point represents one measurable tooth specimen; n refers to the total number measured (two pairs of values are coincident). Analogous results were obtained for the M_1, M_3, and M^1.
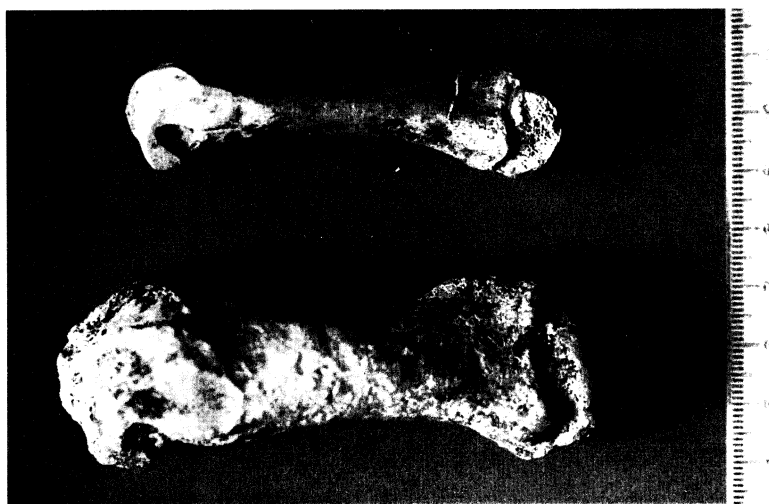
FIGURE 4. Gracile and robust bear fifth metacarpals corroborating the presence of two species (*U. deningeri* and *U. arctos*) in the Yarimburgaz Cave deposits. Scale in cm.

L for Early Pleistocene *U. etruscus* from Saint Vallier defines the small end of each tooth size range shown in Figure 5, whereas the mean L for *U. spelaeus* from Echenoz represents the largest in this comparison. Middle Pleistocene *U. deningeri* samples from Grotte de l'Eglise, Grotte Vaufrey, Nauterie (couche 11), Château, Mosbach, Scharzfeld, and Petralona provide a set of intermediate means in the size range; all of the Kudaro samples (Caves 1 and 3, layers 3–5) are included in the shaded area of the graphs as well, unless indicated otherwise.

The mean L values for the Yarimburgaz cave bear cheek teeth are most consistent with the *U.*

deningeri identification, with the exceptions of the P^4 and M^2 (Fig. 5A). The results show, however, that the Yarimburgaz bears tend toward the larger end of the size range for *U. deningeri*. The P^4 and M^2 in the Yarimburgaz sample are closest in size to those from the Kudaro Caves in the Caucasus, especially the Middle Pleistocene Kudaro sample.

Identification of the Yarimburgaz cave bear can also be explored using a mean tooth size index that counterpoises bucco-lingual breadth and anterior-posterior length ($[B \times 100]/L$), equivalent to that used by Prat (1976: p. 378).

TABLE 2. *Ursus deningeri* cheek tooth size ranges for anterior-posterior (L) and bucco-lingual (B) dimensions.

Tooth element	Type of measurement	Minimum size (mm)	Maximum size (mm)	No. of teeth measured
P_4	L	13.5	17.6	31
	B	8.3	11.3	
M_1	L	25.8	32.1	45
	B	12.7	16.9	
M_2	L	25.4	33.1	64
	B	15.9	20.7	
M_3	L	22.6	31.1	45
	B	15.9	22.0	
P^4	L	17.6	21.9	25
	B	13.3	16.2	
M^1	L	24.4	29.3	30
	B	17.6	21.7	
M^2	L	43.1	50.8	25
	B	21.1	25.9	

Note: Unusually small teeth are omitted from consideration, as these probably represent *U. arctos.*

TABLE 3. Summary statistics for lengths (L) of *U. deningeri* cheek teeth from Yarimburgaz Cave.

Tooth element	No. of observations	Size range (mm)	Mean	SD	SE
a. Size ranges					
P_4	31	13.1–19.4	15.37	1.35	0.24
M_1	45	24.5–32.1	28.04	1.75	0.26
M_2	64	25.4–33.1	29.04	1.59	0.20
M_3	45	22.6–31.1	26.01	2.13	0.32
P^4	25	17.6–21.9	19.64	1.21	0.24
M^1	30	24.4–29.3	26.77	1.34	0.24
M^2	25	42.2–50.8	44.77	1.87	0.37

Tooth element	No. of observations	Minimum	Maximum	Mean	SD	SE
b. Indexed B/L values for upper second molars and lower fourth premolars						
P_4	31	54.6	72.9	63.01	4.65	0.83
M^2	25	46.2	54.8	50.24	2.35	0.47

Note: The index is calculated as ($B \times 100$)/L, corresponding to the index ($VL \times 100$)/MD described by Prat (1976:p. 378).
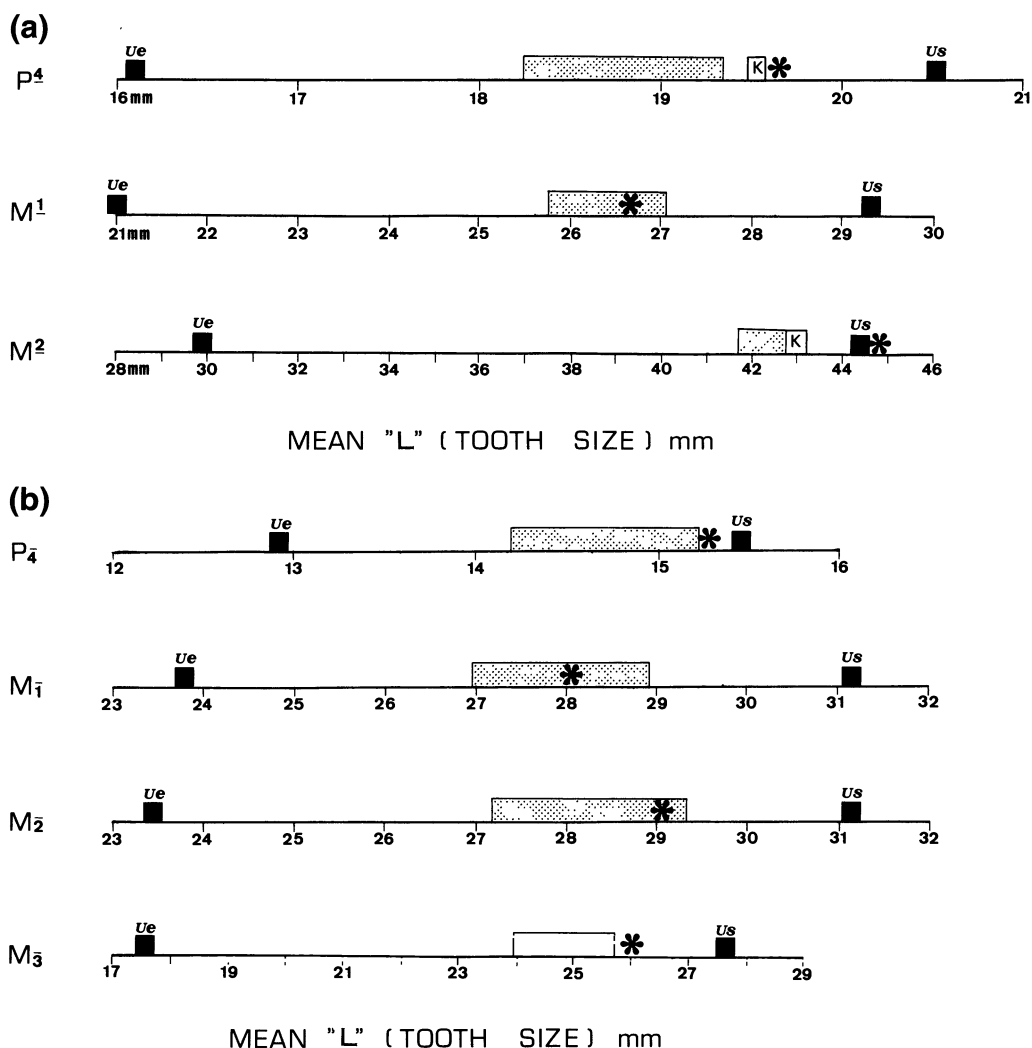
FIGURE 5. Comparison of mean lengths (L) of Yarimburgaz cave bear upper (A) and lower (B) cheek teeth with those of bears from paleontological sites in Greece, France, Germany, and the Transcausasus region. (*Ue*) is the mean size for *U. etruscus* from early Pleistocene deposits of Saint Vallier; (*Us*) for *U. speleaus* from late Pleistocene deposits of Echenoz (early Würm); (*) for the larger bear species from Yarimburgaz Cave. Data for cases other than Yarimburgaz are taken from Prat's compilations (1988: p. 295) and from Baryshnikov (1977) (the Kudaro Caves). The range of means for middle Pleistocene *U. deningeri* assemblages (indicated by a stippled bar) is based on bears from Grotte de l'Eglise, Grotte Vaufrey (lower couches), Nauterie (couche 11), Mosbach (see Laville et al. 1972; Prat 1976; Prat and Thibault 1976), Petralona (see Kurtén and Poulainos 1981), Château (see Argant 1980), and Scharzfeld (see Schütt 1968). Middle and late Pleistocene *U. deningeri* samples from Kudaro Caves 1 and 3 are also included in the shaded bar unless indicated otherwise (K). The bears from Yarimburgaz Cave best fit the *U. deningeri* classification. The measurements for the P⁴ and M² are notable exceptions, however. The Yarimburgaz bears display an overall tendency toward the larger end of the size range for this middle Pleistocene species. Mean lengths for the Yarimburgaz P⁴ and M² are most similar to coeval (middle Pleistocene) samples from Kudaro Caves 1 and 3 in Transcausasia, though larger.

The indexed values for the P_4 and M^2 (Table 3b) of the Yarimburgaz bears—the enigmatic teeth in the previous comparison—fall *within* the range of French Middle Pleistocene *U. deningeri* as defined by Prat (1976, planche I), not with *U. spelaeus*. Specifically, the mean index for Yarim-burgaz P_4s is indistinguishable from that for *U. deningeri* from couche 11 of Nauterie. Likewise, the mean index for Yarimburgaz M^2s is about the same as those for *U. deningeri* from Nauterie and Grotte de l'Eglise.

We conclude that the two species of bear in

the middle Pleistocene deposits of Yarimburgaz Cave are a small-bodied from of *U. arctos* (rare), and a comparatively large-bodied population of *U. (a.k.a. Spelearctos) deningeri*. The *U. deningeri* cave bears from Yarimburgaz were considerably larger than those from Petralona (cf. Kurtén and Poulainos 1981), and larger than but most similar to those from the more distant Kudaro Caves 1 and 3 in the Transcausasus. The apparent *U. deningeri* specimens from the newly discovered Alma Bear's Cave in northern Israel (Tchernov and Tsoukala 1997), also middle Pleistocene in age, are too few for statistical comparisons, but it is clear that they were much smaller-bodied than the Yarimburgaz population. Chronospecies designations for cave bears cannot be reliable measures of time in regions where the cave bears are poorly known. The morphologic indications of *U. deningeri* (as opposed to *U. spelaeus*) nonetheless are in agreement with independent geomorphological assessments of the lower cave sediments (Farrand 1992) and preliminary electron-spin-resonance dates obtained from mammal teeth (Blackwell et al. 1990).

Hibernation-Related Mortality and Postmortem Bone Damage

The age structure of the cave bear assemblage from Yarimburgaz displays a classic attritional pattern: a bimodal or U-shaped configuration if plotted in two-dimensional graphic format. Two distinct peaks occur in age cohorts III and VIII (Fig. 6). The mortality pattern differs from the structure of a living population (or random deaths therein) primarily because of the near absence of prime-aged adult bears in the death assemblage. The age scoring technique, reference data on modern bear life history characteristics, and results of the mortality analysis summarized here (Table 4) are presented in Stiner (1998). An interesting detail of the mortality pattern of the cave bears is the prominence of older juveniles among the immature age cohorts (cohort III, Table 4a, Fig. 6), a substantial proportion of which probably perished during the first winter of independence from their mothers; the low proportion of individuals in cohort I may be due to a low probably of pres-
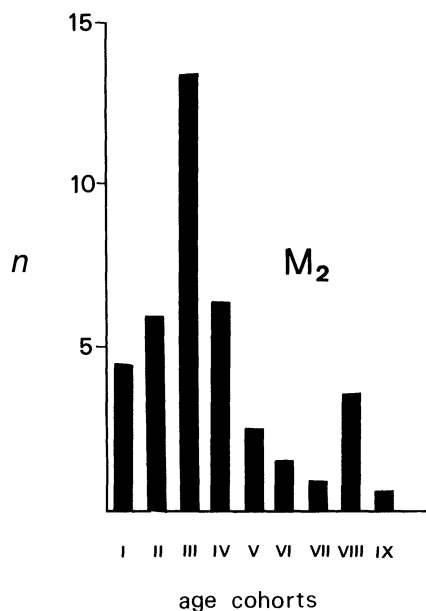

FIGURE 6. Age structure histogram for the Yarimburgaz bear death population, showing nine age cohorts based on the M_2 (from Stiner 1998); *n* represents the number of individuals. The age structure displays a bimodal, or U-shaped, contour centering on cohorts III and VIII in this two-dimensional format. The mortality pattern indicates a relative paucity of prime-aged adults in relation to the normal structure of a complete living population. Juveniles in cohort III are especially prevalent, possibly representing deaths following / during the first winter of independence. The much lower proportion of cohort I may be partly due to the possibility that the crowns of some individuals in this age group were not yet fortified by a dentin base; but this would not have been true for cohort II.

ervation for enamel caps not yet fortified by dentin, but this would not be true for teeth assigned to cohort II. The high proportion of individuals in cohort III is consistent with the situation among modern brown bears of North America (see, for example, Glenn et al. 1976; Bunnell and Tait 1981). That mid-row cheek teeth were completely demolished by occlusal wear in some instances (Stiner 1998) shows that some of the bears lived a long time (about 6% of all individuals), although a gritty diet is likely to exaggerate the wear effect (see below).

The U-shaped mortality pattern in the Yarimburgaz cave bears, along with nearly complete skeletal representation (excluding tooth counts), are consistent with hibernation-related death patterns arising primarily from starvation. The U-shaped mortality pattern differs

TABLE 4. Nine-cohort mortality data for Yarimburgaz bears based on the most prevalent cheek tooth elements (from Stiner 1998).

Tooth element	No. of age-scored teeth	MNI*	Age cohorts								
			I	II	III	IV	V	VI	VII	VIII	IX
a. Nine age cohort format for most abundant molar elements											
M^1	43	25	8	6	11	5	2	0	1	8	2
M_1	65	35	5	6	20	13	.7	5	1	4	4
M_2	79	44	9	12	27	13	5	3	2	7	1
M_3	62	39	7	13	15	7	4	4	3	7	2

Tooth element	No. of age-scored teeth	% Juvenile	% Prime adult	% Old adult
b. Compressed three-age cohort format, with idealized age structure models†				
Living-structure mortality—ideal		34	45	21
U-shaped (attritional) mortality—ideal		59	22	19
Juvenile-biased mortality—ideal		71	29	0
P^4	37	62	35	3
M^1	43	58	19	23
M^2	36	67	14	19
M_1	65	48	40	12
M_2	79	61	29	10
M_3	62	56	29	14

* The number of age-scored teeth includes right and left elements. The minimum number of individual animals (MNI) is based on the most common side (right or left); it is not used for any of the calculations to follow but instead is provided as background information.

† See Stiner 1994: pp. 292–295, 316–330 for the bases of the models. The values representing each of the three models do not include information on normal variation associated with them. The best overall match is between the U-shaped (attritional) model and the Yarimburgaz data (Stiner 1998).

significantly from randomly selected age groups in hibernation dens (Stiner 1998) and therefore cannot be the cumulative result of surprise attacks by hominids, wolves, or hyenas. Bear bones are much less often damaged by carnivore gnawing than ungulate and non-ursid carnivore remains in the cave (Stiner et al. 1996: p. 298); there are no tool (cut) marks. What damage occurs on the bear bones is attributable to non-ursid large carnivores (wolves and/or hyenas) and occasional cannibalism by other bears (e.g., Fig. 7A). Hunted bears cannot be distinguished from scavenged ones on the basis of bone damage, but the mortality pattern argues strongly for the latter interpretation.

Relatively high frequencies of rodent gnawing (e.g., Fig. 7B) and mild weathering (stage 1 of Behrensmeyer [1978]) occur on the bear bones, in contrast to the condition of other large mammal remains, implying that the bear skeletons lay exposed on the cave floor for longer periods and suffered fewer mechanical disturbances than other species' bones on the average. All of these observations are consistent with the hibernation scenario. They also show that the circumstances in which the bear remains accumulated were distinct from those responsible for other animal remains in the cave (Stiner et al. 1996).

Tooth Damage and Skeletal Pathologies during Life

Koby (1940, 1953) noted peculiar wear and breakage on the anterior teeth of some European cave bears. He proposed that the damage occurred during life and was caused at least partly by ingestion of coarse materials and mineral-laden clays. The condition of canines and incisors of some of the Yarimburgaz cave bears from Turkey shows that the phenomenon is geographically widespread. Many of the Yarimburgaz cave bear canines were broken or chipped during life and greatly worn through continued use. Many were also seriously damaged by interstitial wear and abrasive forage (e.g., Fig. 7D). The damage to the front teeth tends to be idiosyncratic in form and location, and it occurs on 31% of all adult canines that had come into wear prior to death. The damage suggests habitual plowing through dirt while foraging, consumption of tough, gritty foods and minerals, and yanking on abrasive material. The Yarimburgaz cave bears also show an overall pattern of extensive occlusal attrition common to cave bears in
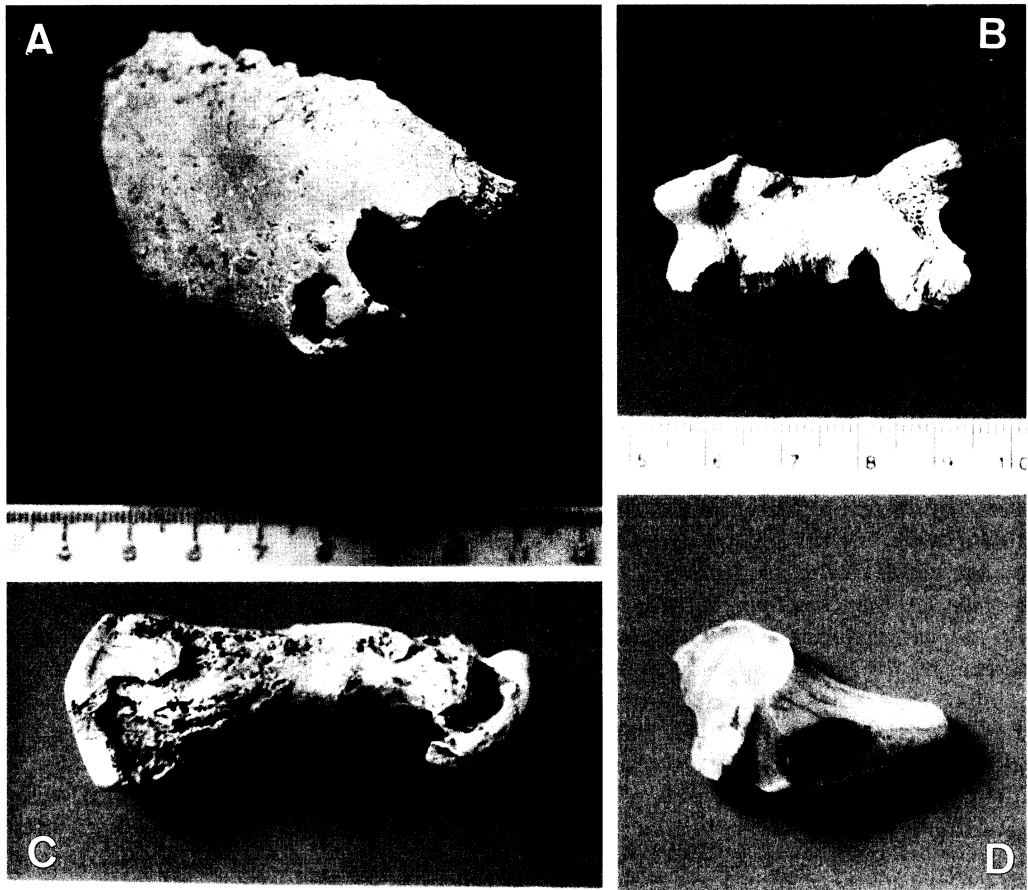
FIGURE 7.   Cave bear remains. A, Young bear frontal bone fragment punctured by the incisors of a large adult bear.
B, One of many phalanges extensively gnawed by small rodent, suggesting that the bear skeletons lay on the ground
surface for some time before being buried in sediment. C, pathological surfaces on bear third metacarpal, probably
a form of osteoarthritis. D, Canine distorted (in this instance) by non-occlusal wear. Scale in cm.

general, due apparently to habitual grinding
of tough foods and analogous to what has
been observed for other cave bears (Barysh-
nikov 1997; Kurtén 1976: pp. 18ff).

Bone pathologies occur with some frequen-
cy on the lower limb bones of some of the
adult cave bears (3% of all identified bones).
The pathologies fall into two categories,
healed bone fractures (trauma) and what ap-
pears to be advanced osteoarthritis, evidenced
by scab-like formations on nonarticulating
surfaces (e.g., Fig. 7C) and polished joint sur-
faces. Nearly all bone pathologies occur on
foot elements, especially metapodials, and the
presumed osteoarthritis is ten times more
common than evidence of healed trauma.

Moreover, the afflictions are asymmetrically
distributed. The healing and scarring mani-
fest on the bones demonstrates that these in-
dividuals survived for considerable periods
despite their afflictions.

Because the affected bones were disassoci-
ated from teeth when found, it is not possible
to link pathologies directly to age at death in
individual bears, or to whole skeletons. How-
ever, the incidence of both arthritis and healed
trauma in bears is concentrated in just four ex-
cavation units (Stiner et al. 1996). It therefore
is likely that most pathological specimens
originated from just a few animals, because a
strong correlation exists in the spatial distri-
bution of the two kinds of bone pathologies. A

systemic association between healed trauma and osteoarthritis is to be expected, since the healing process alters an animal's locomotor patterns, shifting stress loads throughout the body and promoting the development of arthritis in certain other joints and extremities (E. Trinkaus, A. Grauer personal communications 1993; see also Wainwright et al. 1976; Currey 1984).

Sex Ratio and Size Dimorphism of *U. deningeri*

Attempts to determine the sex ratio and extent of size dimorphism of a jumbled fossil population is not unlike looking for structure in a bowl of pudding. Nonetheless, there are ways of examining the Yarimburgaz assemblage that yield strong evidence, if not perfectly crisp answers, on these two interesting population characteristics. For reasons explained below, the adult sex ratio is an indirect indicator of bear paleodiet. Size dimorphism in a bear population, on the other hand, potentially reflects aspects of its socioecology; size difference between the sexes will vary among populations, however, as a curvilinear function of average body mass.

Large fossil samples representing many individuals of both sexes and spanning multiple proveniences are required for sex ratio and size dimorphism analyses, because the nesting space requirements of adult males and females may differ somewhat with stature and whether dependent young are present (Reynolds et al. 1976; Judd et al. 1986; see also Kurtén 1976: p. 77; Andrews and Turner 1992). The cave bear assemblage from the lower chamber of Yarimburgaz Cave fulfills these sampling requirements in that it is a large collection, recovered from many excavation trenches spread over an area of 70 by 20 meters (see Arsebük et al. 1990; Arsebük and Özbaşaran 1994; Stiner et al. 1996). Naturally, all of the methods applied below must be appropriate to disassembled skeletons, including isolated teeth.

In the *sex ratio analysis,* the number of juvenile bears must also be controlled, because young individuals in modern bear populations normally hibernate with their mothers during the first, second, and, in some cases,

third winters of life (reviewed in Stiner 1998). Juvenile cohorts can substantially bias a bear sex ratio in hibernation contexts because mothers give birth to roughly even proportions of male and female cubs on the average (Rogers 1987), and the hibernation schedules of juvenile males and females parallel that of reproducing adult females (e.g., Craighead et al 1976; Glenn et al. 1976; Bunnell and Tait 1981; McNamee 1984; Murie 1985). In contrast to the sex ratio at birth, the adult sex ratio of a living bear population is subject to considerable imbalance with adulthood, favoring females in some contexts (e.g., Craighead et al. 1974; Rogers 1987).

Juveniles can also distort perceptions of *size dimorphism* between the sexes if bone (as opposed to tooth) measurements are used. The pivotal consideration is the point when a skeletal element stops growing, schedules for which vary by body part and hard tissue type. In the case of bones, juvenile specimens were identified and removed from the Yarimburgaz data set on the basis of tissue porosity, size, and rugosity. Eruption and occlusal wear status were used to identify juveniles from teeth. Identification and exclusion of immature individuals on the basis of tooth eruption and wear is more clear-cut, because permanent enamel crowns reach a fixed size quickly. Hence teeth are favored for the sex ratio analysis below, but not for analyzing size dimorphism, which requires attention to weight-bearing members.

Adult Sex Ratio.—Gordon and Morejohn (1975) present a useful technique for identifying bear sex ratios, developed and tested using four known-sex control populations of black bear (*U. americanus*) from western North America. Although not originally formulated as such, the technique can also be applied to disarticulated fossil cave bears. Their approach uses the anterior–posterior length of the mandibular canine *alveolus* and the breadth (B) of the second mandibular molar crown for segregating male and female bears of a given population. Among tooth elements, the permanent canines are especially sensitive indicators of sex in bears (see also Koby 1949; Kurtén 1958, 1976). The M_2 is less sensitive but helps further separate the sexes in a bi-direc-

TABLE 5. Apparent sex ratio and size dimorphism of Yarimburgaz Cave bears based on linear measurements of the mandibular canine and second molar, with and without juveniles. n represents the number of measurable individuals presumed to be of each sex. The mean value is based on a linear measurement (mm) of the anterior-posterior length (L) of the mandibular canine crown.

Age range	Females		Males		
	n	Mean	n	Mean	M/F
All years	22	19.5	20	22.2	0.91
w/o <1 yr.	18	19.4	15	22.0	0.83
w/o 0–2½ yrs.	11	19.5	8	22.2	0.73

tional plot of the two measurements. The technique is effective as long as one subspecies or population is considered in isolation from all others; dental variations among modern bear subspecies and species disallow mixing or compounding of samples. Although a different sort of bear is involved in the Yarimburgaz study, this fossil sample fulfills the stipulations set by Gordon and Morejohn's (1975) method in that it represents a single species of cave bear (*U. [Spelearctos] deningeri*) from a restricted time range and place. Also, lower canines (C_1) and lower second molars (M_2) of cave bears are relatively abundant in the Yarimburgaz sample (Table 5). Brown bear (*U. arctos*) teeth in the sample are easily excluded from consideration because of their much smaller dimensions.

Some modifications of Gordon and Morejohn's approach are necessary, however, in order to apply it to the Yarimburgaz cave bear sample. Because the alveolus surrounding the C_1 was often damaged or destroyed, an anterior–posterior (L) measurement of the base of the C_1 crown must be substituted for Gordon and Morejohn's alveolus measurement (1975: p. 41). Another problem arises from the fact that many of the cave bear teeth were separated from mandibular bone by postdepositional disturbances. Our inability to consistently match teeth to individuals in the Yarimburgaz sample is remedied by (1) size-ordering the measurements for the two kinds of teeth independently of one another, (2) creating C_1-M_2 pairs based on the size order, and then (3) fine-tuning the matches using side and eruption-wear status of the teeth (the latter based on control information on intact

tooth rows [see Stiner 1998]). This solution emulates individuals in the absence of certainty. It has the unfortunate effect of eliminating the inter-individual size variation that normally exists in natural populations, hence producing a falsely linear arrangement of points in the distribution that should not be taken for a true correlation. However, the procedure does preserve the fundamental size gap between males and females sought here.

The plot of cave bear C_1 and M_2 measurements in Figure 8 reveals two apparently distinct groups of points, presumably representing female and male teeth (right and left sides combined). Individual C_1-M_2 pairs are distinguished on the graph according to age, with open symbols for juveniles and solid symbols for adults. More significant than the exact position of the inferred female-male dividing line is the fact that a slight bias in favor of female bears for the entire death population (0.91 males to females) is amplified (0.83 and 0.73 respectively) with the removal of two consecutive juvenile cohorts (Table 5). In essence, male frequencies decline more rapidly than those for females as the juvenile age categories are subtracted. The proposed gap between the sexes also increases when only adult bears (solid points) are considered.

An adult sex ratio of 73 male cave bears to every 100 females (73:100) in the Yarimburgaz sample has important implications for cave bear ecology in the study area. The sex ratio in European cave bear samples varies between 39:100 and 100:100 males to females but most large samples tend to be relatively even (summarized in Kurtén 1976: pp. 76–77). The sex ratio of the Yarimburgaz cave bears from Turkey is consistent with those of the European samples. The dietary significance of the adult sex ratio is rooted in female bears' tendency to produce generally even proportions of male and female young, all of whom are confined to dens in winter. However, the sex ratio of mature bears perishing in dens may be swayed toward females (a) to the extent that the living proportion of hibernating adults is so and (b) the degree to which adult bears other than pregnant females depend on plants and invertebrates for food. The probability of individual bear deaths inside dens, and thus
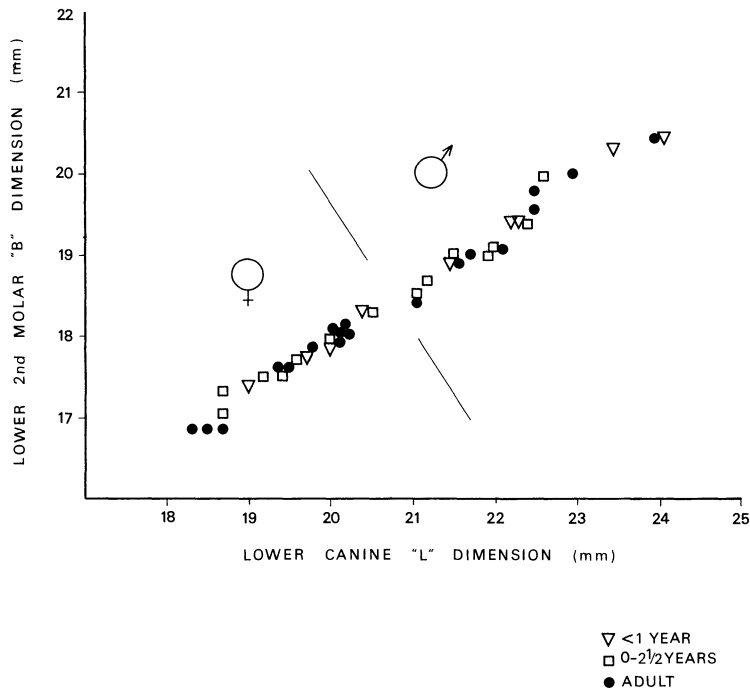
FIGURE 8.   Bi-directional plot of mandibular canine and second molar measurements of Yarimburgaz cave bears showing two distinct clusters, presumably representing female and male teeth. The data points do not represent articulated dentaries but instead are reconstructed artificially from the two sets of measurements, rank ordered by size to form C_1-M_2 pairs, refined with the aid of age and side information; the peculiarly strong linear correlation is merely an artifact of the size-ranking procedure. The gap separating the sexes is significant despite the procedure and indicates only slight skewing in favor of female cave bears. The female bias is stronger, however, when two successive juvenile age cohorts (<1-year-olds, then 0–2.5-year-olds) are removed from consideration (summarized in Table 5). The gap between the sexes increases when only adult bears (solid symbols) are compared.

the frequency of individuals by age and sex, is partly a function of time spent in these places. Diet greatly influences the duration of hibernation, which in modern bears varies from about seven months to almost no time at all (e.g., Rogers 1987: pp. 20–24; Helgren et al. 1990: p. 291; Johnson and Pelton 1980).

All pregnant female bears in modern circumstances must hibernate for several months in order to allow their cubs to develop and become mobile (e.g., Johnson and Pelton 1980). In contrast, adult males and barren adult females need only hibernate as long as food is unavailable. A predominantly seasonal food supply pushes the adult sex ratio in hibernation death assemblages toward evenness. Reliance on meat from large game in winter (see Picton and Knight 1986 for a related discussion), the part of the year when bears cannot find plants, invertebrates, and most small vertebrates, will amplify the female bias beyond

that already present in the living population. Males of a relatively herbivorous population should have hibernation times approaching those of pregnant females; female bias in den deposits would therefore decline with bears' increasing emphasis on seasonally available foods.

Available information on the diet and sex ratios of modern hibernating bears may help us interpret the variation in sex ratios we observed in the fossil species. Rogers (1987: p. 13) reports that the sex ratio for young black bears in Minnesota is approximately equal, but that only one third of the adults were males (M/F about 50:100). Because we know black bears to be highly omnivorous and to hibernate for up to seven months, we would infer from a similar adult sex ratio in paleontological cases a heavy dependence upon seasonal plant and invertebrate foods. A greater dietary emphasis on large mammals (scav-

enged or hunted) instead should result in even greater differences between pregnant female and adult male hibernation times, and, consequently, the different probabilities in the bones of males and females becoming part of fossil assemblages in caves. Modern polar bears, which are fully carnivorous, represent the opposite extreme in that adult males may not hibernate at all and therefore would not normally die in dens (i.e., about 0:100 M/F).

The sex ratio of 73 males to every 100 females in the Yarimburgaz cave bears displays only slight skewing toward females among the adults, and it lies at one extreme of the full range of natural patterns. The mild female bias in hibernating cave bears lies within the range typical of the highly omnivorous black bear in North America but is more even than most. The sex ratio results on the Yarimburgaz sample suggest two related conclusions about the *U. deningeri* cave bears: (1) the living population was not poor in adult males and (2) these animals depended heavily upon highly seasonal food resources such as nuts, hard-coated seeds, tubers, berries, grasses, insects, eggs, and the like. The latter conclusion is entirely consistent with the appearance of the cave bear's dental specializations (Kurtén 1976; Baryshnikov 1997), which include many cusps per tooth and large occlusal surfaces in relation to crown height, apparently devoted to grinding functions. Whether the Yarimburgaz cave bears were firmly committed to the vegetarian end of the dietary continuum is unclear, but a dedication to highly seasonal food sources is clear from these data. The sex ratio specifically contradicts the possibility of a regular, heavy emphasis on large game.

Size Dimorphism between the Sexes.—Determining the extent of size dimorphism in adult cave bears depends foremost upon isolating skeletal measures that accurately reflect differences in lean body mass, taking into account the mathematical relations among linear (a), square (areal, or a²), and cube (mass or a³) functions in terrestrial vertebrates. Modern bears exhibit comparatively high levels of size dimorphism between the sexes, most conspicuously in adult stature and weight. Grossly analogous patterns have been inferred for Pleistocene cave bears of the Northern Hemi-

sphere on the basis of measurements of weight-bearing bones of the extremities and canine teeth (e.g., Koby 1949; Kurtén 1958, 1976). For analysis, the developing bones and teeth of immature animals again must be identified and removed from consideration, in this case because they exacerbate the tendency of measurement data to form a continuous size gradient, with no separation between the sexes. Two different carpal or wrist bones— the scapholunate and the pisiform—of the bear forelimb are emphasized for the size dimorphism analysis here, because carpals experience direct, regular loading during movement. The growth and maintenance of these bones therefore registers long term changes in a bear's weight.

Two perpendicular measurements ("1" and "2" in Fig. 2B,C) were taken on the scapholunates and pisiforms and examined in linear and area-scaled comparisons. Various premolars and molars are similarly employed, although they can only provide conservative estimates of body size difference. The mandibular canine data discussed in the previous section, for example, show that the canine bases of male cave bears were 1.138 times longer than those of females on average. The cubed product of the linear value suggests that adult males were roughly 1.47 times the mass of adult females on the average. However, even canine measurements, though clearly subject to sexual selection, can underestimate differences in complete body mass of adult male and female bears, because their dimensions are not directly constrained by the mechanical stresses of locomotion. The canine-based estimate discussed here also lacks thorough consideration of the effects of sample size and overlapping size distributions of the two sexes.

Josephson et al. (1996) recently developed a more comprehensive approach to estimating sexual size dimorphism in living and fossil vertebrate populations, using the "method-of-moments" (MoM). It is applied here to a variety of carpal and dental elements for which side of the body is known; canine data could not be included in this analysis because wear and breakage too often obliterated indications of side. The MoM procedure assumes that the

total distribution of a metric trait is composed of two underlying normal distributions, one for males and one for females. Three moments around the mean of the combined-sex distribution are used to estimate the means and the common standard deviation of the two underlying distributions. Advantages of the technique include the facts that the sex of each individual in the population need not be known in advance and that no reference to living species analogs is required. Right and left elements were analyzed separately to avoid counting individuals twice.

Ideal populations for MoM analysis are those whose male and female distributions overlap minimally to moderately—bears certainly qualify. Simulations used to test the MoM approach show that it is more accurate and reliable than other published methods of estimating size dimorphism (reviewed in Josephson et al. 1996). While larger sample sizes (>15 individuals) produce clearer results, small samples also provide some information about sexual size dimorphism. In general, larger samples yield more reliable estimates and narrower confidence intervals, even when the underlying sex ratio is moderately skewed (Josephson et al. 1996). The Yarimburgaz sample sizes for measurements of various carpal and dental elements fall on either side of the 15-individual threshold.

Tables 6 and 7 list MoM linear and areal estimates for upper and lower premolars and molars, and scapholunates and pisiforms, as the ratio of male mean to female mean. Sample sizes and the minimum and maximum boundaries of the 95% confidence interval are also given; no reliable maximum estimate could be calculated for the smallest samples. It is clear from Figures 9 and 10 that the carpal measurements provide the highest linear and areal estimates of size dimorphism in the Yarimburgaz cave bear sample. The MoM values based on linear scapholunate measurements range between 1.23 and 1.37 (Table 6), meaning that those of adult males are 1.2 to nearly 1.4 times longer or wider across the articular surface than those of adult females. The product of the two perpendicular measurements yields an "areal" MoM value of 1.61 for rights and 1.75 for lefts (Table 7). Should these re-

TABLE 6.   Size dimorphism one-dimensional (linear) estimates by method-of-moments (MoM) for adult Yarimburgaz Cave bears, based on carpal and dental elements.

Tooth or carpal element	Side	Measurement type*	n	MoM†	Minimum	Maximum
Teeth						
P⁴	L	L	11	1.11	1.05	1.27
P⁴	L	B	12	1.10	1.05	1.19
P⁴	R	L	14	1.11	1.07	1.19
P⁴	R	B	14	1.10	1.05	1.19
M¹	L	L	16	1.10	1.06	1.16
M¹	L	B	16	fourth moment > 3.0‡		
M¹	R	L	14	1.09	1.06	1.15
M¹	R	B	14	1.09	1.00	1.16
M²	L	L	17	fourth moment > 3.0		
M²	L	B	16	1.11	1.05	1.16
M²	R	L	8	1.07	1.06	na
M²	R	B	9	fourth moment > 3.0		
P₄	L	L	16	fourth moment > 3.0		
P₄	L	B	16	1.15	1.08	1.25
P₄	R	L	16	1.14	1.05	1.21
P₄	R	B	17	1.18	1.07	1.31
M₁	L	L	22	1.11	1.06	1.16
M₁	L	B	22	1.10	1.00	1.20
M₁	R	L	23	1.09	1.00	1.14
M₁	R	B	27	1.12	1.07	1.17
M₂	L	L	39	1.05	1.00	1.09
M₂	L	B	42	1.09	1.06	1.12
M₂	R	L	25	1.13	1.09	1.17
M₂	R	B	26	1.16	1.13	1.21
M₃	L	L	22	fourth moment > 3.0		
M₃	L	B	22	fourth moment > 3.0		
M₃	R	L	24	1.19	1.14	1.24
M₃	R	B	24	fourth moment > 3.0		
Carpals						
Scapholunate	L	1	12	1.30	1.23	1.51
Scapholunate	L	2	12	1.37	1.27	1.64
Scapholunate	R	1	15	1.23	1.17	1.42
Scapholunate	R	2	15	1.31	1.26	1.55
Pisiform	L & R	1	25§	1.22	1.09	1.33
Pisiform	L & R	2	25§	1.25	1.20	1.32

* See Figure 2 for measurement key.
† MoM refers to the method-of-moments estimate of dimorphism, expressed as the ratio of males to females (M/F). "Minimum" and "maximum" refer to corresponding boundaries of the 95% confidence interval; "na" means that the maximum estimate is not available because the sample size is too small.
‡ No estimate could be made because the fourth moment of the distribution was greater than 3.0.
§ Left and right not distinguished in data set.

sults be extrapolated to yet a third scale of measurement, analogous to body volume or mass, adult male cave bears would have been roughly twice the body weight of adult females. The results obtained from the MoM approach are in general agreement with Kurtén's estimates for cave bears (1976: p. 25) derived by alternative means, though more precise. Interestingly, the degree of size dimorphism in the cave bears is not very different from that

TABLE 7. Size dimorphism two-dimensional (areal) estimates by method-of-moments (MoM) for adult Yarimbur-gaz Cave bears, based on carpal and dental elements.

Tooth or carpal elements	Side	Measurement type*	n	MoM†	Minimum	Maximum
Teeth						
P^4	L	L × B	11	1.21	1.10	1.41
P^4	R	L × B	14	1.21	1.08	1.33
M^1	L	L × B	15	1.16	1.01	1.26
M^1	R	L × B	14	1.17	1.06	1.30
M^2	L	L × B	16		fourth moment > 3.0‡	
M^2	R	L × B	8	1.08	1.05	na
P_4	L	L × B	16	1.25	1.00	1.47
P_4	R	L × B	16	1.25	1.00	1.47
M_1	L	L × B	22	1.22	1.00	1.34
M_1	R	L × B	22	1.17	1.00	1.30
M_2	L	L × B	39	1.16	1.09	1.21
M_2	R	L × B	25	1.28	1.20	1.38
M_3	L	L × B	22		fourth moment > 3.0	
M_3	R	L × B	24	1.36	1.25	1.51
Carpals						
Scapholunate	L	1 × 2	12	1.76	1.54	2.60
Scapholunate	R	1 × 2	14	1.61	1.47	2.00
Pisiform	L & R	1 × 2	23§	1.55	1.39	1.78

* See Figure 2 for measurement key. Areal (two-dimensional) osteometric traits are products of two measurements: anterior-posterior length (L) × buccolingual breadth (B) for teeth; measurement 1 × measurement 2 for carpal bones.
† MoM refers to the method-of-moments estimate of dimorphism, expressed as the ratio of males to females (M/F). "Minimum" and "maximum" refer to corresponding boundaries of the 95% confidence interval; "na" means that the maximum estimate is not available because the sample size is too small.
‡ No estimate could be made because the fourth moment of the distribution was greater than 3.0.
§ Left and right not distinguished in data set.

found in large-bodied modern brown bears living in northern latitudes (Kurtén 1958).

Paleodiet of the Yarimburgaz bears: Carbon and Oxygen Isotopes in Fossil Enamel

The carbon isotopic composition of fossil apatites and collagen has been used extensively in paleodietary reconstructions for land and sea mammals (see review by Koch et al. 1994). Collagen has received the most attention because its carbon and nitrogen isotopic composition can be used in combination to distinguish land from marine dietary sources, as well as herbivory from carnivory. Fossil apatites are also useful and are preserved on a time scale of millions of years, although the issue of postdepositional isotopic exchange is still widely debated. It is clear that postdepositional changes in the carbon (C) and oxygen (O) isotopic composition of fossil bone mineral can occur (Schoeninger and DeNiro 1982; Nelson et al. 1986); however, fossil tooth enamel does preserve an original dietary signal, at least partly because of its dense, coarsely crystalline nature (Lee-Thorp and van der Merwe 1987; Lee-Thorp et al. 1989; Thackeray et al. 1990; Quade et al. 1992).

This section examines the carbon and oxygen isotopic composition of the enamel of the middle Pleistocene cave bears (*Ursus deningeri*) and brown bears (*U. arctos*) from Yarimburgaz Cave to address several questions: Has the original isotopic composition of the bear tooth enamel been altered since burial? If not altered, what were the major dietary preferences of the bears, and do cave and brown bears in the sample differ? Did either kind of bear consume substantial quantities of marine foods such as anadromous fish? It would also be useful to know the extent to which either species depended upon terrestrial plants for food (as opposed to meat), but this requires $\delta^{15}N$ analysis of collagen, which has not been performed on these samples.

Methods for the Isotope Analyses.—Enamel pretreatment and analysis follow procedures formulated by Lee-Thorp and van der Merwe (1987), modified by Quade et al. (1992). The enamel was cleanly detached from the dentin of each tooth with a high speed drill. The enamel was then ground to a powder sufficiently fine to pass through a 125-mesh sieve, immersed in 2% NaOCl for two hours to re-
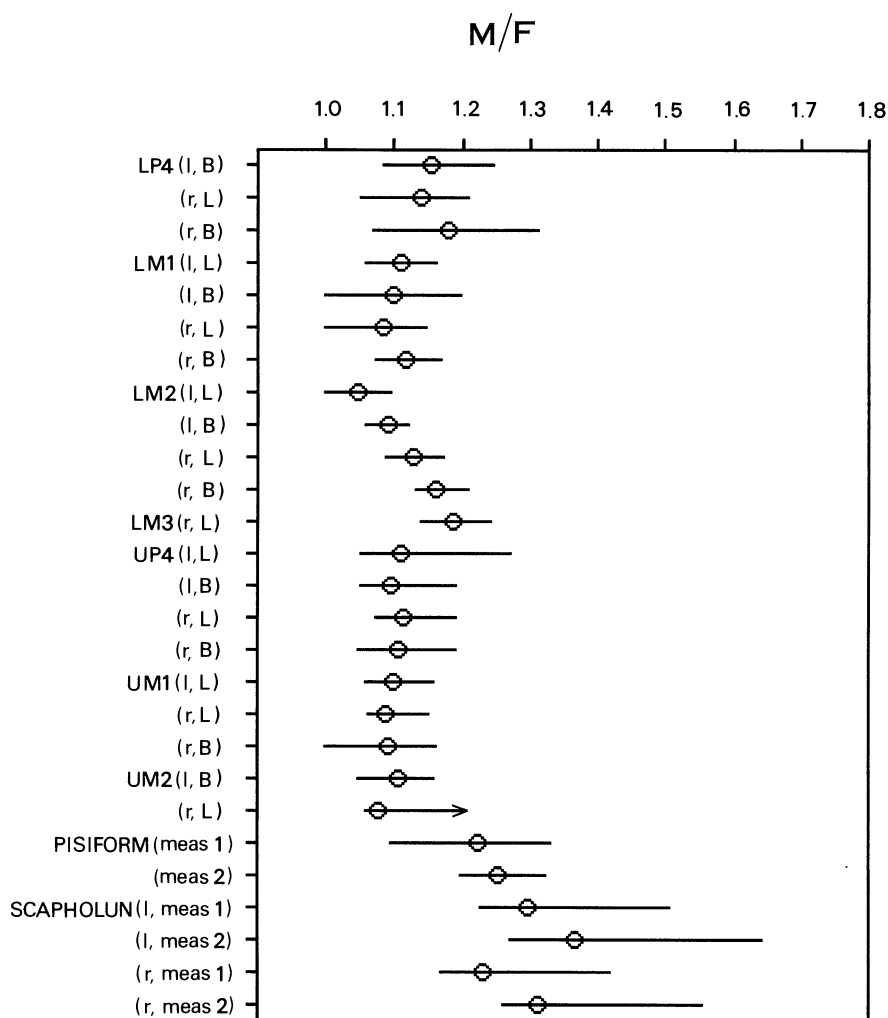
M/F

FIGURE 9. One-dimensional (linear) method-of-moments (MoM) results on size dimorphism in adult cave bears (male mean/female mean, M/F) from Yarimburgaz Cave, based on various cheek teeth, pisiforms, and scapholunates (weight-bearing carpal bones). Measurement codes and orientations as in Figure 2. The open circle represents the MoM estimate; the line is the 95% confidence interval; a line terminating with an arrow means that only a minimum estimate could be obtained; (r) right side; (l) left side. The carpal measurements yield the highest linear estimates of body size dimorphism between the sexes.

move organic matter, and rinsed thoroughly in distilled water.

Biological apatites are non-stochiometric analogs of hydroxyapatite [$Ca_{10}(PO_4)_6(OH)_2$]. Small amounts of carbonate ions are present in hydroxyapatite in two positions: one as "structural carbonate" substituting for PO_4 and to a lesser extent for OH^- (Elliot et al. 1985), and the second as "nonstructural carbonate" adsorbed onto mineral surfaces (Betts et al. 1981). In order to isolate the more tightly bonded structural carbon and oxygen for iso-

topic analysis, the samples were reacted for 6–12 hours in 1M acetic acid, which removes nonstructural C from the surfaces of the apatite crystals. Dried samples were then reacted with 100% phosphoric acid at 25°C, thereby liberating the structural carbon and oxygen. The isotopic analyses were performed mainly on a Finnigan Delta S gas-source mass spectrometer. Results for both carbon and oxygen are presented in the usual δ notation, as the per mil (‰) deviation of the sample CO_2 from the PDB standard, where
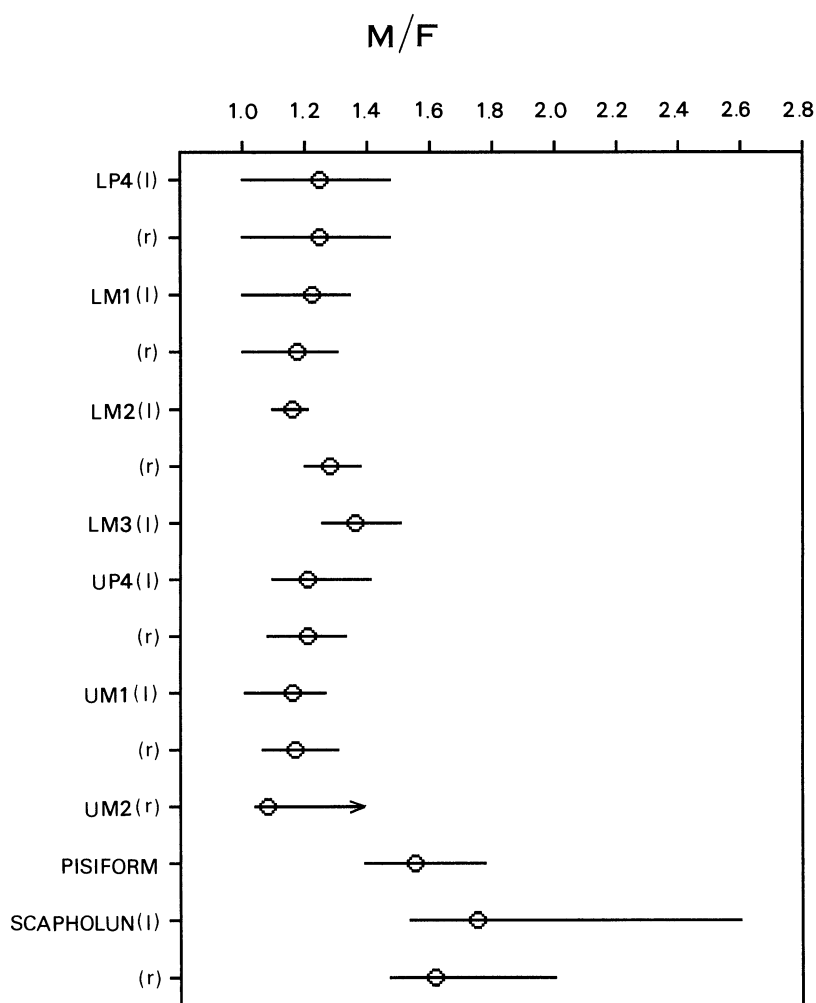
FIGURE 10. Two-dimensional (areal) method-of-moments (MoM) results on size dimorphism in adult cave bears (male mean/female mean, M/F) from Yarimburgaz Cave, based on various cheek teeth, pisiforms, and scapholunates (weight-bearing carpal bones). The open circle represents the MoM estimate; the line is the 95% confidence interval; line terminating in arrow means that only a minimum estimate could be obtained; (r) right side; (l) left side. Again, the carpal data provide the highest estimates of body size dimorphism between the sexes and, because the bone elements are subjected directly to locomotor stresses during life, more accurately reflect areal differences in body mass. A simple cube projection of the results suggests that adult males were double or greater the lean mass of adult females on the average.

$$R = {}^{13}C/{}^{12}C \text{ or } {}^{18}O/{}^{16}O, \quad \text{and}$$

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000.$$

Twenty-three separate teeth were analyzed, 21 of cave bears and 2 of brown bears, the results for which are shown in Table 8.

Results on Enamel Diagenesis and Paleodiet.— The carbon analyses yielded a mean $\delta^{13}C$ (PDB) value of -15.1 ± 0.7‰ and a range of -14.1 to -16.4‰. The results from the brown bears, although deriving from only two teeth,

are essentially indistinguishable from those for the cave bears (Table 8). The oxygen analyses indicate an average value of -6.5 ± 1.0‰ in $\delta^{18}O$ (PDB) and a range of -4.9 to -9.0‰.

Some postdepositional alteration of bone probably goes on in all settings, no matter how arid or recent. Alteration of isotopic composition is a separate issue that must be dealt with on a site-by-site basis. Two lines of evidence suggest that the fossil material from Yarimburgaz Cave retains its original carbon isotopic imprint. The evidence on oxygen,

TABLE 8. Isotopic composition results for Yarimburgaz bear tooth enamel samples.

Specimen no.	$\delta^{13}C$	$\delta^{18}O$ (PDB)	% CaCO³	% C
Ursus deningeri				
1290	−14.1	−6.6	5.66	0.68
224	−15.9	−6.9	4.97	0.60
393	−14.7	−6.6	4.15	0.50
40/198	−16.1	−6.2	5.13	0.62
38	−14.3	−8.2	4.87	0.58
620	−15.5	−5.2	4.97	0.60
37	−15.1	−6.5	4.71	0.57
178	−15.0	−6.6	4.23	0.51
40	−15.0	−6.6	—	—
625	−15.5	−9.0	5.32	0.63
815	−14.5	−5.2	5.12	0.61
1300	−14.4	−6.3	5.28	0.63
913	−15.2	−5.8	4.75	0.57
222	−15.7	−6.8	5.05	0.61
192	−14.6	−6.2	4.50	0.54
651	−15.6	−6.3	5.43	0.65
273	−15.2	−5.0	5.39	0.64
125	−16.1	−5.8	5.12	0.61
43	−15.2	−7.1	4.45	0.53
472	−14.3	−7.7	5.46	0.65
27	−14.4	−7.9	4.62	0.55
Ursus arctos				
1275	−14.3	−5.3	5.20	0.62
644	−16.4	−4.9	4.47	0.53

while less complete, also argues against alteration.

With regard to the carbon composition, the teeth from Yarimburgaz Cave have not undergone any clear loss of structural carbon since burial. The fossil teeth average 0.59 ± 0.05% C (or about 4.9% CaCO₃), within the range displayed by modern teeth (Brudevold and Soremark 1967; Tochon-Danguy et al. 1980; Rey et al. 1991). This evidence contradicts the possibility of isotopic changes caused by addition or loss of carbon. Moreover, the carbon isotopic range of −14.1 to −16.3‰ displayed by the Yarimburgaz bear enamel samples is within the range expected for modern terrestrial animals feeding on plants in the circum-Mediterranean region. The observed fractionation factor for ^{13}C between pretreated carbonate in bone apatite is about 12–13‰ in most modern herbivores and carnivores (Sullivan and Krueger 1981; Lee-Thorp and van der Merwe 1987). This would yield a $\delta^{13}C$ value for cave bear diet of −25 to −29‰. Such an estimate is quite consistent with isotope ranges displayed by the C_3 plants that dominate Eu-

rope and the circum-Mediterranean region today.

Carbon isotopic results for modern herbivores feeding on virtually pure C_3 plant biomass in Alaska, Nova Scotia, and Finland (Pigati 1996) provide additional points of comparison: nearly all of the $\delta^{13}C$ values fall between −13 and −17‰, also similar to the Yarimburgaz bears (Fig. 11). This is not the range expected for enamel that has been altered by waters percolating through a cave system. The bedrock that contains Yarimburgaz Cave is composed of limestone, and most limestones display $\delta^{13}C$ values between −2 and +2‰. Subsurface water will begin to exchange with this carbon below the soil zone, which in turn may lead to alteration of fossil apatites buried in cave sediments. The close correspondence between the expected and measured $\delta^{13}C$ values in tooth enamel argues strongly against postburial alteration of the Yarimburgaz samples.

The $\delta^{18}O$ values of the Yarimburgaz bear tooth enamel samples are not inconsistent with values expected for this latitude in a coastal setting. A detailed consideration of the $\delta^{18}O$ results is not warranted given the host of factors other than rainfall that may determine the $\delta^{18}O$ value of biogenic apatite, such as species' metabolic characteristics and surface evaporation rates in the habitat. A more direct and useful test would be to compare the fossil readings to those for modern bears across a latitudinal gradient, but such comparisons have yet to be done.

Both nitrogen and carbon isotopic values can be used to distinguish marine from terrestrial dietary sources. Nitrogen analyses were not performed by us, but carbon composition can be very useful wherever local terrestrial plant communities are composed entirely of C_3 plants. Herbivores and carnivores that consume C_3 plants should average −14 ± 2‰ in $\delta^{13}C$, where local biomass is approximately −27‰ (Fig. 12). End-member carnivores that feed on marine resources (including anadromous fish and possibly sea plants) average −10 ± 2‰ (DeNiro and Epstein 1978, 1981; Chisholm et al. 1982; Koch et al. 1994; Hilderbrand et al. 1996). The range of $\delta^{13}C$ results of −16.3 to −14.1 for bears from Yarim-
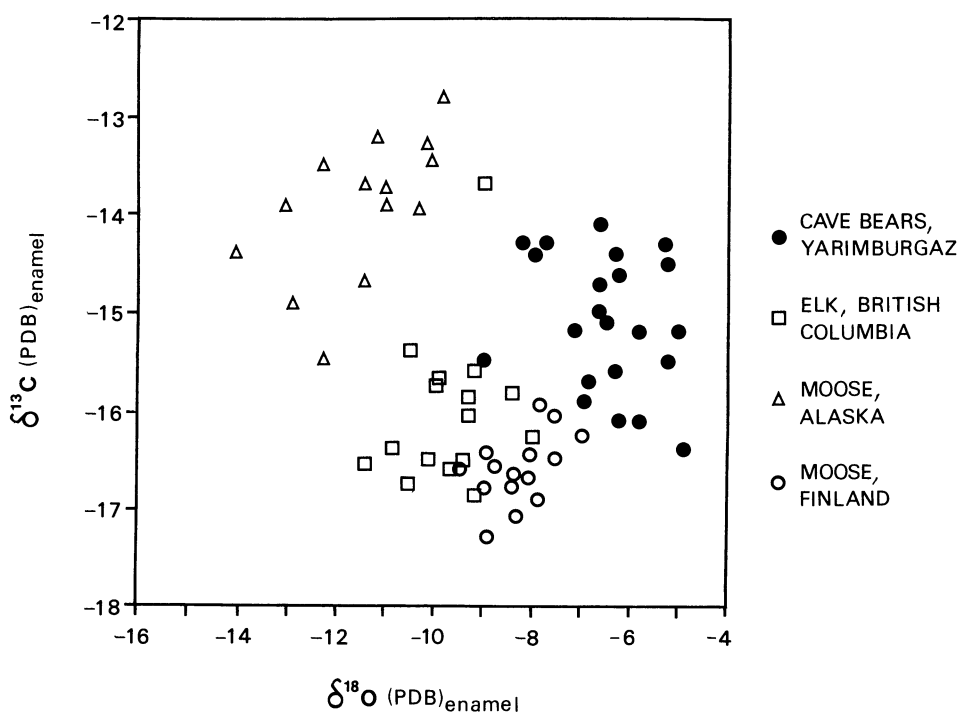
FIGURE 11. The δ^{13}C (PDB) versus δ^{18}O (PDB) of tooth enamel carbonate from fossil bears from Yarimburgaz Cave and large modern herbivores from other regions that fed on C_3 biomass. The overlap of δ^{13}C results suggests that all are drawing on terrestrial food sources in habitats dominated by C_3 vegetation. The δ^{18}O (PDB) results differ greatly among sample populations, consistent with the differing δ^{18}O values of rainfall among regions.

burgaz Cave is well within the range expected for diets dominated by terrestrial C_3 resources, although minor intake of marine sources cannot be precluded by the results.

The Yarimburgaz results can also be compared with those of modern and fossil bears from the Pacific northwest of the United States, Alaska, and western Europe, all regions that today are dominated by C_3 vegetation. Collagen samples from modern brown bears in the Pacific northwest and Alaska display a wide range of δ^{13}C and δ^{15}N values, interpreted to reflect the bears' mixed dependence upon marine (mainly salmon) and terrestrial resources (Matheus 1995; Hilderbrand et al. 1996). The Yarimburgaz cave bears display highly negative δ^{13}C values (after correction for the fractionation factor between collagen and apatite) most consistent with those modern bears feeding on a diet composed largely or entirely of terrestrial food sources.

Our carbon isotope results for the Yarimburgaz bears match very well measurements from some cave bear samples in western Europe (Bocherens et al. 1994; Hilderbrand et al. 1996). Bocherens et al. (1994) obtained δ^{13}C values on cave bear apatite of $-14.8 \pm 0.7\%$ ($n = 15$), remarkably close to those of Yarimburgaz at $-15.1 \pm 0.6\%$ ($n = 21$). Such concordance suggests that the dependence of cave bears on terrestrial food sources was widespread. However, Bocherens et al. (1994) and Hilderbrand et al. (1996) disagreed on the degree of herbivory in cave bears as evidenced by nitrogen isotope measurements. Our isotope results cannot speak directly to this issue, as carbon isotopic values are not good discriminators of trophic level. Other sources of information on the Yarimburgaz cave bears do speak to this issue, however, and strongly contradict a scenario of a high degree of carnivory in this Middle Pleistocene sample from Turkey.

Nitrogen isotopic ratios are the most robust discriminators of trophic levels and therefore of the dietary continuum between carnivory and herbivory. However, such analysis requires well-preserved proteins (collagen or collagen-
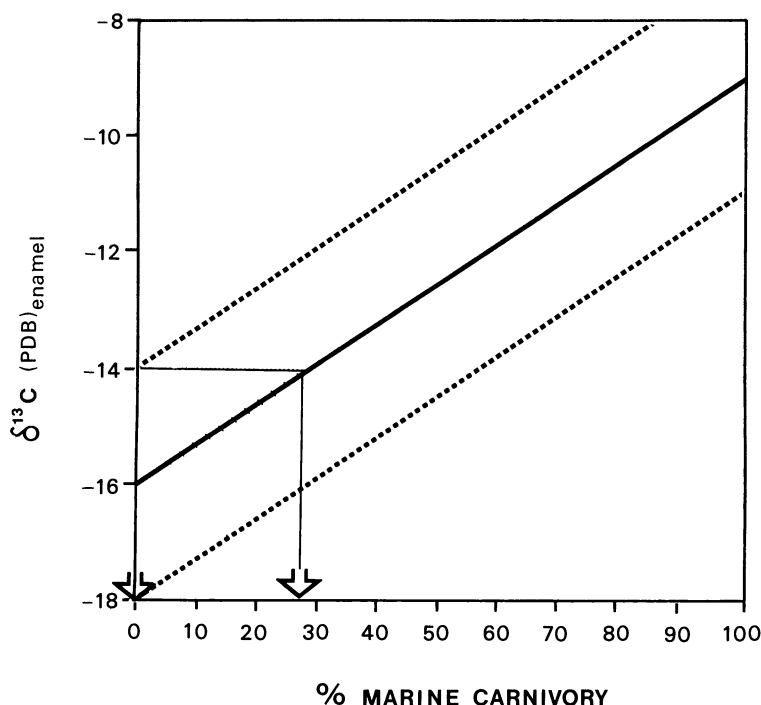
FIGURE 12.   The $\delta^{13}C$ (PDB) of tooth enamel carbonate versus the percentage reliance on marine resources, with the mean (solid line) and range (dashed line) of isotopic values for a range of diets from purely terrestrial to strictly marine (see references cited in text). The shaded area represents the range of the Yarimburgaz bear enamel $\delta^{13}C$ results. The data from the Yarimburgaz bears (both species) imply 75–100% reliance on terrestrial food sources. Even a value of 75% is very likely an underestimate and should be regarded as a minimum, given the 1–2‰ global decrease in the $\delta^{13}C$ (PDB) of atmospheric CO_2 over the last century.

like substances), which are uncommon in most pre-Holocene fossils. Carbon isotopic values are not good discriminators of trophic level, and we therefore cannot differentiate herbivory from carnivory in the fossil bears.

To summarize, the fossil bear teeth from Yarimburgaz Cave retain an unaltered carbon isotopic composition very similar to that of modern herbivores and carnivores living in regions dominated by C_3 vegetation; such a situation presently exists around the Mediterranean Sea. Marine resources were not an important component of the diets of the Yarimburgaz bears, in strong disagreement with results on cave bear samples from western Europe, even though the cave is situated in a near-coastal setting. No significant differences are found between cave and brown bears in the study sample, although it should be noted that only two brown bear teeth were available for analysis. The available isotope data do not

allow us to distinguish between herbivory and carnivory in the bears (but see below).

Discussion

By virtue of a collaboration across disciplines, informed by comparisons of modern bear species, this study provides new information on the paleoecology of extinct cave bears. While the Yarimburgaz study is confined to only one place and time period, we hope that it sets a useful precedent for application to a wider range of cases, so that variation in cave bear habits among regions and species may eventually be known and contradictions among results addressed constructively. Our investigation reveals the following kinds of information about cave bears in western Turkey.

The Middle Pleistocene bears of Yarimburgaz Cave are of two species, the cave bear, *Ursus (Spelearctos) deningeri* (>40 individuals), and the much more gracile brown bear, *U. arc-*

tos (2 individuals). The mortality pattern and the condition of the bear skeletons show that the assemblage is the cumulative result of hibernation-related mortality. The Yarimburgaz cave bears exhibit a size range that is consistent with middle Pleistocene populations of *U. deningeri* from France, Germany, and Greece, although the mean crown lengths of some of the Yarimburgaz cave bear cheek teeth are relatively great, and considerably greater than those from nearby Petralona (Thessalonika). The Yarimburgaz sample best resembles some of the dental dimensions documented by Baryshnikov (1997) for the middle Pleistocene *U. deningeri* samples from the Kudaro Caves (1 and 3) in Transcausasia. The Yarimburgaz case demonstrates that *U. deningeri* cave bears were more widely distributed in West Asia than previously thought (see also Baryshnikov 1996, 1997), perhaps especially in Turkey; their more ephemeral presence in the northern Levant (Israel) may have been restricted to colder phases of the middle Pleistocene (Tchernov and Tsoukala 1997).

Kurtén (e.g., 1976: pp. 18ff; Baryshnikov 1997) reasoned on grounds of dental morphology and inferred musculature that cave bears were more vegetarian than other members of the genus *Ursus*. The body proportions of cave bears, particularly the massive, barrel-shaped torso and short robust lower limbs argue for power at the expense of agility. Multiple lines of evidence concerning cave bear diet at Yarimburgaz Cave reinforce a general picture of an animal heavily dependent upon plant mast and tubers, invertebrates, and other small game. Common to all of these foods is their seasonal pattern of availability—few if any of them can be had in winter. The occluding surfaces of the adult cave bear cheek teeth for Yarimburgaz Cave show extensive attrition caused by habitual grinding of resistant, gritty materials. Researchers have observed this characteristic in other cave bear samples, noting that occlusal wear generally tends to exceed that found in other bear species (Kurtén 1976; Baryshnikov 1997). This no doubt reflects dietary adaptations that were unique to cave bears.

The anterior dentitions (incisors and canines) of old individual cave bears from Yarimburgaz Cave display extensive damage as well, mostly as idiosyncratic breakage, chipping, and wear on non-occluding surfaces. Such damage indicates a combination of foraging and masticatory behaviors, including frequent pulling of coarse, abrasive materials through the front teeth while feeding and using these teeth to remove matrix or hard coverings during the search for hidden or buried foods. The combined patterns of tooth damage therefore reflect the predominantly tough and gritty nature of cave bear diet overall (e.g., tough nut hulls and fibrous tubers), frequently obtained from subterranean or encased sources (e.g., grubs that live under bark or underground). Any suggestion that cave bear teeth were adapted specifically to crushing the bones of large mammalian prey is inconsistent with the results of comparative research on the dental morphologies of the Carnivora (e.g., Van Valkenburgh 1989).

A seasonal, vegetarian/invertebrate emphasis in the diet of the middle Pleistocene cave bears from northwest Turkey is also indicated by the *adult* sex ratio, which is only slightly biased toward females. Denning schedules and durations of modern bears are known to vary according to sex, individual age, and the extent to which the food supply is seasonal. The near-even proportions of adult male and female cave bears in the large sample from Yarimburgaz Cave indicates that adult males spent nearly as much time in hibernation caves as did adult females. An equal sex ratio, or one that is only slightly skewed toward females, shows that hibernation was an essential overwintering strategy for both sexes because of the powerful influence of seasonal food supplies. The sex ratio of the Yarimburgaz cave bears strongly contradicts the expectations for highly carnivorous bears, and particularly a dietary dependence on large mammals.

The Yarimburgaz cave bears display a high degree of sexual size dimorphism. The wrist bones of these animals, which would have experienced heavy mechanical loading during life, indicate that mature males often attained a mass twice or greater than that of adult females. However, this pattern is not very different from modern, large-bodied populations of brown bears. Similar levels of size dimorphism between the two phylogenetic groups

may indicate that the mating strategies of cave bears during the middle and late Pleistocene were not very different from those of modern brown bears. The phenomenon merits continued research, both on the patterns manifest by fossil bears and the physiologic consequences of mating strategies in modern bears.

Also interesting is the apparent coexistence of cave and brown bears in many Pleistocene environments; time-averaging effects can undermine perceived species associations in paleontological records but this widespread association is robust. The differing morphologies of cave and brown bear dentitions argue for considerable niche separation between these phylogenetic groups, yet carbon and oxygen isotopic analyses of cave and brown bear tooth enamel samples from Yarimburgaz give essentially identical readings with regard to predominant food sources. Perhaps the isotopic signals are too coarse for this purpose, providing more information about the ecosystem in which these animals lived than about relatively subtle differences in the lifeways of the two kinds of bears. The lack of a substantial marine signal in bear diets in the vicinity of Yarimburgaz Cave is surprising in light of the site's present situation near an estuary of the Marmara Sea. While the Black Sea may have undergone some radical changes in salinity levels over time, the possibility that Yarimburgaz Cave was associated with a primarily fresh-water (as opposed to marine) hydrology during the middle Pleistocene is contradicted by the presence of one sea urchin spine and one oyster shell in general association with the cave bear remains. We conclude from the isotope results that both kinds of bears in Yarimburgaz Cave were principally terrestrial and fresh water foragers, more so than brown bears that periodically feed on large game and/or migratory salmon today (cf. Hilderbrand et al. 1996).

A final point on cave bear paleoecology arises from the observation that cave bear remains, originating from hibernation-related mortality, coincide in the middle Pleistocene deposits of Yarimburgaz Cave with Paleolithic stone artifacts left by archaic humans. Hominids' and bears' interests in using the shelter overlapped, but they probably never inhabited it simultaneously. Cave bears certainly were hibernators (e.g., Kurtén 1958, 1976; Stiner et al. 1996; Stiner 1998), and the exceptional vulnerability that all bears experience while hibernating would have made them very shy of any shelter where disruption was likely (on modern bears see, among others, McNamee 1984; Murie 1985; Rogers 1987). Occupations of Yarimburgaz Cave by bears and humans (and other shelter-using species) no doubt were widely scattered in time and hinged upon a low risk of interference. The situation in Yarimburgaz Cave is not unusual for middle and some late Pleistocene cave faunas of Eurasia, or for sites that contain Acheulean or Mousterian (Middle Paleolithic) artifacts. However, most of these early examples pose a stark contrast to the faunal records of Eurasian shelters dating to more recent Paleolithic culture periods (Gamble 1986; Stiner 1993, 1994: pp. 6–9). Many later sites, especially after the Last Glacial Maximum of roughly 18,000 years ago, seem to be dominated either by human refuse to the near exclusion of other biogenic refuse, whereas other shelters of the same age contain materials left mostly by carnivores. The emphemeral occupations by hominids of early Paleolithic cave sites suggest that archaic human populations were much smaller than those of the mid-Upper Paleolithic onward, and bears may have been relatively more prevalent.

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